

From the Institute of Physiology and Biophysics
University of Lund
Sweden

CLIMBING AND MOSSY FIBER PATHS
TO CEREBELLAR ANTERIOR LOBE
ACTIVATED FROM DORSAL FUNICULUS

BY
BENGT LARSON

LUND 1979

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AKADEMISK AVHANDLING

som med vederbörligt tillstånd av Medicinska fakulteten vid
Lunds Universitet för avläggande av medicine doktorsexamen
kommer att offentligens försvaras å Fysiologiska Institutionens
stora föreläsningssal måndagen den 21 maj 1979 kl. 9¹⁵.

av

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Med.kand., Mlm.

Lund 1979

Organisation LUND UNIVERSITY Institute of Physiology Sölvegatan 19 S-223 62 Lund, Sweden		Document name DOCTORAL DISSERTATION Date of issue 1979-05-21 CODEN: LUMEDW/(MEFF-1003) 1-157 (1979)	
Author(s) Bengt Larson		Sponsoring organisation	
Title and subtitle CLIMBING AND MOSSY FIBER PATHS TO CEREBELLAR ANTERIOR LOBE ACTIVATED FROM DORSAL FUNICULUS			
		A4	A5
Abstract Comparison of climbing (dorsal spino-olivocerebellar paths, DF-SOCs) and mossy (cuneocerebellar tract, CCT) fiber paths activated from dorsal funiculus. Field potentials in the cerebellar cortex and activity in single CCT cells evoked on nerve stimulation were recorded in anesthetized cats. The DF-SOCs terminate in sagittal zones in the cerebellar anterior lobe. Four zones are activated by cutaneous and high threshold muscle afferents through paths with disynaptic relays in dorsal funiculus nuclei (DFN) and direct connections from DFN to inferior olive (IO). Two zones are activated by distal cutaneous afferents through indirect paths with neurons intercalated between DFN and IO. The DF-SOC projections to some zones have a detailed somatotopical organization. The proprioceptive component of CCT (P-CCT) is monosynaptically activated by group I muscle afferents and originates from the external cuneate nucleus, whereas the exteroceptive component (E-CCT) is di- and polysynaptically activated by cutaneous and high threshold muscle afferents and originates from the rostral part of the main cuneate nucleus. E-CCT terminates in superficial parts of cerebellar cortex and P-CCT in deep parts. E-CCT terminates in five sagittal zones which overlap five of the zones activated by DF-SOCs. In some zones the E-CCT projection has a detailed somatotopical organization which overlaps that of the DF-SOC. The information carried by DF-SOCs and CCT, the termination, and possible roles in motor control were discussed.			
			
Key words		A4	A5
Classification system and/or index terms (if any)			
Supplementary bibliographical information			Language English
ISSN and key title			ISSN
Recipient's notes		Number of pages 157	Price
		Security classification	

Distribution by (name and address) **Bengt Larson, Institute of Physiology, University of Lund, Sölvegatan 19, S-223 62 Lund, Sweden**

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This thesis is based on the following articles which will be referred to by their Roman numerals:

- I. Cooke, J.D., Larson, B., Oscarsson, O., Sjölund, B.: Origin and termination of cuneocerebellar tract. *Exp. Brain Res.* 13, 339-358 (1971)
- II. Cooke, J.D., Larson, B., Oscarsson, O., Sjölund, B.: Organization of afferent connections to cuneocerebellar tract. *Exp. Brain Res.* 13, 359-377 (1971)
- III. Ekerot, C.-F., Larson, B.: Differential termination of the exteroceptive and proprioceptive components of the cuneocerebellar tract. *Brain Res.* 36, 420-424 (1972)
- IV. Ekerot, C.-F., Larson, B.: The dorsal spino-olivocerebellar system in the cat. I. Functional organization and termination in the anterior lobe. Accepted for publication in *Exp. Brain Res.*
- V. Ekerot, C.-F., Larson, B.: The dorsal spino-olivocerebellar system in the cat. II. Somatotopical organization. Accepted for publication in *Exp. Brain Res.*
- VI. Ekerot, C.-F., Larson, B.: Termination in overlapping sagittal zones in cerebellar anterior lobe of mossy and climbing fiber paths activated from dorsal funiculus. Submitted for publication.

INTRODUCTION

The cerebellar cortex contains five main types of neurons which are organized in a strictly geometrical pattern (Eccles et al., 1967). Four types of neurons, the Purkinje, Golgi, basket and superficial stellate cells are inhibitory, whereas one type of neuron, the granule cell is excitatory. The axons of the Purkinje cells, the only efferent cortical neurons, exert an inhibitory action on the neurons of the intracerebellar nuclei. The cerebellum receives two main kinds of afferent fibers, climbing fibers (CFs) and mossy fibers (MFs). Both CFs and MFs give off excitatory collaterals to the intracerebellar nuclei before terminating in the cortex. The branches of the CFs have a powerful one-to-one excitatory action directly on the Purkinje cells. The MFs excite the granule cells whose axons form the parallel fibers which in large numbers excite the Purkinje cells. The CFs originate mainly or exclusively from the inferior olive (IO), whereas the MFs originate from many nuclei in the brain stem and spinal cord (Szentágothai and Rajkovits, 1959; Oscarsson, 1973; Desclin, 1974; Batini et al., 1976; Matsushita et al., 1979).

The cerebellar cortex has a uniform structure throughout suggesting that different parts process information in a similar way. A functional differentiation is obtained by different areas having different afferent and efferent connections. The cerebellar cortex is divided into transverse and longitudinal divisions which intersect. Three transverse divisions have been identified mainly on the basis of the afferent connections and phylogenetical considerations (Larsell, 1937): archi-(vestibulo-), paleo-(spino-) and neo-(cerebro-)cerebellum. The longitudinal divisions have been identified mainly on the basis of the efferent connections. Jansen and Brodal (1940) showed the existence of three sagittal zones on each side: one vermal zone projecting to the fastigial and lateral vestibular nuclei, one intermediate zone projecting to the interpositus nuclei, and one lateral zone projecting to the dentate nucleus.

Much more elaborate transverse and longitudinal subdivisions have been demonstrated in the anterior lobe which is part of the spinocerebellum and has been extensively studied in the cat.

Classical evoked potential studies showed a transverse subdivision with one rostral area (approximately lobules II-IV) which was activated from hindlimb nerves and one caudal area (approximately lobule V) which was activated from forelimb nerves (Adrian, 1943; Snider and Stowell, 1944). Later studies have demonstrated that the spinal input to the cerebellum is mediated by many CF and MF paths which terminate according to different topographical patterns. Only some paths conform approximately to the classical somatotopical pattern (Oscarsson, 1973, 1976).

The CF paths ascend through different spinal funiculi and terminate in narrow sagittal zones in the cerebellar cortex. Eight zones have been identified on each side of the anterior lobe (Oscarsson, 1969b, 1973, 1976). These zones correspond approximately to the zones identified by Voogd (1969) on the basis of myeloarchitecture and corticonuclear connections. Different zones are innervated from specific parts of the IO (Armstrong et al., 1974; Brodal and Walberg, 1977a, 1977b; Groenewegen and Voogd, 1977; Groenewegen et al., 1979), although some zones are innervated in pairs by branches of the same olivary neurons (Armstrong et al., 1973b; Ekerot and Larson, 1977). Each zone presumably has a separate efferent path through a certain cerebellar nucleus and it has been suggested that each zone is a functional unit controlling a particular motor mechanism (Oscarsson, 1969b, 1973, 1976; Voogd, 1969; Andersson and Oscarsson, 1978a, 1978b; Haines and Rubertone, 1977).

The termination patterns in the anterior lobe of the MF paths have been studied in less detail than those of the CF paths. However recent studies indicate that some MF paths terminate in longitudinal zones, which may be related to the zones activated by the CF paths (Voogd, 1969; Voogd et al., 1969; Künzle, 1975; Vielvoye, 1977).

Thus the synaptic effects of the CF and MF inputs on cortical neurons on the one hand, and the properties of several CF and MF paths on the other, are known from many studies. However, no detailed comparison has been made of specified CF and MF paths terminating in the same area.

The purpose of the present thesis was to compare the peripheral inputs, relays, and terminations of one CF system, the dorsal spino-olivocerebellar paths (DF-SOCs), and of one MF path the cuneocerebellar tract (CCT). These paths are activated from primary afferents ascending in the dorsal funiculus (DF), relay in the dorsal funiculus nuclei (DFN), and terminate in partly overlapping areas in the anterior and posterior lobes of the cerebellum.

METHODOLOGICAL CONSIDERATIONS

The experiments were performed on young adult cats anesthetized with sodium pentobarbital or alpha-chloralose. Detailed methodological descriptions are given in the different papers. Only some general points will be considered here.

The spinal cord was transected at C3 sparing only the DFs. In this preparation other CF and MF paths were interrupted except for an indirect path to the lateral reticular nucleus (Glendenin et al., 1975). Activity in the DF-SOCs and CCT was usually evoked by nerve stimulation. In papers I-III the stimulus strength was graded to identify the groups of afferents which activate different components of the CCT. In papers IV-VI a high stimulus strength (usually 20 times nerve threshold) which was supramaximal for evoking responses in the DF-SOCs and CCT was used. The ascending paths in the DFs were stimulated at C3 to determine the synaptic delays in the pathways (II, IV).

In papers I and II microelectrode recordings were obtained from single units in the cuneate nuclei and the restiform body. The CCT neurons were identified by antidromic activation from the cerebellar surface. Recordings from cell bodies and axons were differentiated by the shape and size of the spike potentials.

In papers III-VI field potentials were recorded from the cerebellar anterior lobe. Recordings were obtained from the cerebellar surface with a silver ball electrode or from the molecular and granular layers with a microelectrode. Climbing fiber potentials evoked through the DF-SOCs were recorded as characteristic nega-

tive potentials in the molecular layer or as corresponding positive potentials at the cerebellar surface (Eccles et al., 1967). Mossy fiber potentials evoked through the CCT were recorded as negative potentials in the granular layer generated by activity in granule and Golgi cells, or as later negative potentials in the molecular layer generated by activity in parallel fibers and in dendrites of Purkinje cells and inhibitory interneurons (Eccles et al., 1967). In paper III recordings were also obtained from single Purkinje cells.

The locations of microelectrode tracks and recording sites in the anterior lobe and in the cuneate nuclei were assessed by values read on the micromanipulator during the experiments and from reconstructions made from histological sections. The cerebellar lobules were identified according to Larsell (1953).

ABBREVIATIONS

a, b, x, c ₁ , c ₂ , c ₃ , d ₁ , d ₂	termination zones in anterior lobe
C3	third cervical segment of spinal cord
CCT	cuneocerebellar tract
CF	climbing fiber
DF	dorsal funiculus
DFN	dorsal funiculus nuclei
DSCT	dorsal spinocerebellar tract
E-CCT	exteroceptive component of CCT
ECN	external cuneate nucleus
IO	inferior olive
MCN	main cuneate nucleus
MF	mossy fiber
P-CCT	proprioceptive component of CCT
SOCp	spino-olivocerebellar path
VF	ventral funiculus

RESULTS AND COMMENTS

A. DORSAL SPINO-OLIVOCEREBELLAR PATHS

In the original study on the DF-SOCP it was assumed that it was a single homogenous path (Oscarsson, 1969a). In paper IV it was demonstrated that the DF-SOCP is a compound system consisting of several paths (DF-SOCPs) with different functional organization and termination. The DF-SOCPs projected to eight sagittal zones on each side of the anterior lobe (IV, Fig. 4A). Three zones (a, x and b) were identified in the vermis and five (c_1 , c_2 , c_3 , d_1 and d_2) in the pars intermedia. The zones were denoted with letters and indices using a nomenclature modified after Voogd (1969). The a and b zones which are activated from hindlimb nerves only (Oscarsson, 1969a) have not been studied in detail.

Some zones activated by the DF-SOCP system have also been identified in the pyramis and in the paramedian lobule (Armstrong et al., 1973a, 1973b; Oscarsson and Sjölund, 1977b). The projection areas in the anterior and posterior lobes are largely innervated by branches of the same olivary neurons.

1. Organization of pathways (IV).

a. Direct DF-SOCPs.

The shortest response latencies in the x, c_1 , c_3 and d_2 zones and anatomical findings (Boesten and Voogd, 1975; Groenewegen et al., 1975, 1979; Berkley and Hand, 1978) demonstrate that these zones are activated by direct paths monosynaptically connecting the DEN with the IO. Latency measurements indicated that the paths in the DF consist of fast conducting primary afferents in agreement with previous conclusions (Oscarsson, 1969a) but suggested a disynaptic rather than a monosynaptic relay in the DEN.

The x, c_1 , c_3 and d_2 zones are partly innervated in pairs by common pools of olivary neurons which branch to innervate adjacent zones as shown in paper VI, Fig. 5B (Armstrong et al., 1973b; Ekerot and Larson, 1977, 1979).

b. Indirect DF-SOCs.

The responses in the c_2 and d_1 zones had long latencies indicating that they were evoked through indirect paths with neurons intercalated between the DFN and the IO. This is in agreement with anatomical studies, which have shown that those parts of the IO which innervate the c_2 and d_1 zones do not receive direct fibers from the DFN (Boesten and Voogd, 1975; Groenewegen et al., 1975, 1979; Berkley and Hand, 1978). The preolivary relays are unknown but presumably located in the lower brain stem since long latency responses in the c_2 and d_1 zones have been observed on stimulation of the DF in decerebrate preparations (Larson et al., 1969).

Responses in the c_2 zone were only obtained in preparations anesthetized with chloralose, whereas responses in the d_1 zone were obtained in both preparations anesthetized with pentobarbital and chloralose.

In preparations under chloralose anesthesia the short latency responses in the x , c_1 , c_3 and d_2 zones were followed by additional long latency responses which were presumably evoked through indirect paths. These paths which are activated by distal cutaneous afferents in ipsilateral nerves were not studied in detail.

2. Afferent input (IV) and topographical organization of termination zones in the anterior lobe (V).

a. Direct DF-SOCs.

The direct DF-SOCs projecting to the x , c_1 , c_3 and d_2 zones were activated by cutaneous afferents and high threshold muscle afferents in ipsilateral nerves.

The x zone which was located in the caudal part of lobule V was activated from forelimb nerves only. It consisted of a narrow homogenous strip which was activated from cutaneous nerves innervating the ulnar side of the forearm and paw and from distal and proximal muscle nerves. The c_1 , c_3 and d_2 zones had detailed somatotopical organizations with the hindlimb represented rostrally, and the forelimb caudally in each zone. The forelimb parts of the c_1 and c_3 zones were mainly located in lobule V which is the clas-

sical forelimb area (Adrian, 1943; Snider and Stowell, 1944), whereas the forelimb part of the d_2 zone was located more rostrally in lobules III and IV (Fig. 4A in paper IV).

The somatotopical organization of the c_3 zone was studied in detail by stimulation of a large number of cutaneous nerves. This zone contained a systematic representation of the entire ipsilateral body surface (V, Fig. 4). Single nerves projected to one or two narrow sagittal strips within the zone. The strips activated from different nerves were partly overlapping and occurred in an order usually following the segmental innervation. The double representation of some nerves made it possible to distinguish one medial and one lateral part of the zone with the projection areas organized approximately as mirror images.

b. Indirect DF-SOCPs.

The indirect DF-SOCPs projecting to the c_2 and d_1 zones were activated by distal cutaneous afferents.

Responses in the c_2 zone were mainly obtained in lobule V. This zone was activated from both forelimb and hindlimb nerves and had no distinct somatotopical organization. The projection from forelimb nerves was bilateral which is a unique feature among the DF-SOCPs.

The d_1 zone was activated from ipsilateral nerves. This zone had largely separate forelimb and hindlimb areas which were mainly located in lobules V and IV, respectively. The responses in the forelimb area were evoked from nerves innervating the ulnar and ventral parts of forepaw.

B. CUNEOCEREBELLAR TRACT

Anatomical and physiological studies indicate that the CCT is the forelimb equivalent of the dorsal spinocerebellar tract (DSCT, Jansen and Brodal, 1958; Grant, 1962a, 1962b; Holmqvist et al., 1963). The CCT is an ipsilateral path which consists of one proprioceptive component (P-CCT) activated by group I muscle afferents and one exteroceptive component (E-CCT) activated by cutaneous afferents.

1. Origin (I).

Anatomical investigations have indicated that the CCT originates from the external cuneate nucleus (ECN, Jansen and Brodal, 1958; Grant, 1962b). In paper I it was confirmed that the P-CCT originates from the ECN, whereas the E-CCT, unexpectedly, was found to originate from the rostral part of the main cuneate nucleus (MCN). In the ECN a distinct somatotopical organization was found with distal to proximal muscles represented in an orderly sequence from dorsomedial to ventrolateral parts of the nucleus (cf. Liu, 1956; Johnson et al., 1968; Rosén, 1969; Campbell et al., 1974). A somatotopical organization has been demonstrated in the rostral part of the MCN (Shriver et al., 1968; Keller and Hand, 1970; Basbaum and Hand, 1973) but this was not detected (cf. 3. Termination). Practically all cells in the ECN projected to the cerebellum and were identified as P-CCT neurons. In the MCN, E-CCT neurons were intermingled with lemniscal neurons and neurons with unidentified termination. A projection from the rostral part of the MCN to the cerebellum has been confirmed in recent anatomical studies (Cheek et al., 1975; Rinvik and Walberg, 1975).

2. Afferent input (II).

a. P-CCT.

The vast majority of the P-CCT neurons was monosynaptically activated by group I muscle afferents. About 60% of these neurons received additional excitation from group II muscle afferents. * A few P-CCT neurons were activated mainly or exclusively by group II afferents. The P-CCT neurons were activated from one muscle nerve only. Using natural stimulation of muscle receptors Rosén and Sjölund (1973a, 1973b) demonstrated that the group I activated P-CCT neurons consist of two separate groups, one activated by group I muscle spindle afferents and one by tendon organ afferents. These authors stretched individual wrist muscles and found that most P-CCT neurons were activated from a single muscle. A few neurons were activated from a couple of adjacent synergists. Also in the rat P-CCT neurons have been shown to be activated from single muscles (Campbell et al., 1974). The P-CCT neurons received postsynaptic inhibition from muscle nerves not supplying

excitation (II). This has been studied in more detail by Rosén and Sjölund (1973a, 1973b) who found many different combinations of excitation and inhibition from various wrist muscles.

Stimulation of the sensorimotor area of the cerebral cortex evoked inhibition in some P-CCT neurons.

b. E-CCT

The E-CCT neurons were di- and polysynaptically activated by cutaneous afferents (II). Using natural stimulation, three subgroups have been identified (Holmqvist et al., 1963, paper II): a) The great majority of the units has a fast adapting response to bending of hairs and a slowly adapting response to touch and pressure. Most of these neurons receive additional excitation from high threshold muscle afferents. b) Units activated exclusively from pressure receptors in pads. c) Units activated exclusively from hair receptors. In paper II the existence of a fourth subgroup having a slowly adapting response to touch and pressure but no fast adapting response to bending of hairs was suggested. It was further found that the excitation from high threshold muscle afferents in some E-CCT neurons originated from rapidly adapting receptors that were sometimes activated by pressure against deep structures but seldom from slowly adapting stretch receptors in muscle.

The receptive fields of the E-CCT neurons determined on natural stimulation were of small to moderate size (1-30 cm²). On the other hand, the majority of the E-CCT neurons were activated on stimulation several skin and muscle nerves. The degree of convergence was less when only short-latency excitation from cutaneous nerves was considered, which is presumably more directly related to the receptive field than the long-latency excitation from skin and muscle nerves.

Stimulation of the sensorimotor area of the cerebral cortex evoked excitation and/or inhibition in some E-CCT neurons.

3. Termination (I, III, VI).

In paper I the termination of the CCT neurons was assessed by the antidromic activation of the MF terminals from the cerebellar

surface. Two projection areas were demonstrated. In the anterior lobe the CCT neurons terminated mainly in the pars intermedia of lobule V and in the paramedian lobule mainly in the four rostral folia. The majority of the CCT neurons send one branch to each area. Similar projection areas have been reported in anatomical studies (Grant, 1962b; Cheek et al., 1975; Rinvik and Walberg, 1975). Grant, Rinvik and Walberg also demonstrated the existence of a third area located in a deep part of the posterior vermis.

More details in the termination patterns were revealed in papers III and VI in which mapping of the MF field potentials in the anterior lobe was made. In paper III it was demonstrated that the E-CCT projects mainly to the superficial parts of the cortex at the apices of the folia, whereas the P-CCT projects mainly to the deep parts of the cortex in the sulci. This has been confirmed in an anatomical study (Rinvik and Walberg, 1975). It is interesting that also other MF paths which relay proprioceptive information terminate in deep parts of the spinocerebellum. This has been shown for the projection from the central cervical nucleus (Wiksten, 1979) which presumably carries proprioceptive information (Abrahams et al., 1976) from the neck, and for a short-latency vestibular input probably consisting of primary and/or secondary vestibular afferents (Precht et al., 1977). On the other hand, a pontocerebellar projection has been shown to terminate preferentially in superficial parts of the cortex (Voogd, 1967).

In agreement with anatomical observations (Voogd, 1969; Voogd et al., 1969) it was demonstrated that the CCT terminates in sagittal zones (VI). The E-CCT terminated in the superficial cortex in five sagittal zones which closely overlapped the forelimb parts of the zones activated by the DF-SOCPs with the conspicuous exception of the d_1 zone (VI, Fig. 5). The x zone and the most lateral part of the c_1 zone were weakly activated by the E-CCT, whereas the medial part of the c_1 zone and the c_2 , c_3 and d_2 zones were strongly activated. The E-CCT projection to the c_3 zone was activated from the entire forequarter and had a detailed somatotopical organization which was similar to and overlapped that of the DF-SOCP. The medial part of the c_1 zone and the d_2 zone were not studied in detail but the results suggest that

these zones have a similar organization as the c_3 zone. The E-CCT projection to the c_2 zone was activated from the paw.

The P-CCT also terminated in sagittal zones. This path projected to the deep parts of the c_1 , c_2 and c_3 zones (III and unpublished observations, the x and d_2 zones were not investigated). These zones were all activated from both distal and proximal muscle nerves. There was no medio-lateral separation of the projections from different muscles. However, distal muscles tended to be represented more superficially in each zone than proximal muscles.

The termination zones of the CCT described above were established by recording the postsynaptic potentials evoked by the MFs in the granular layer. The activity evoked through the CCT in the molecular layer was more widespread due to the conduction along the parallel fibers. The activity in the molecular layer could be distinguished about one mm outside the termination zones in the granular layer suggesting an effective length of the parallel fibers of about two mm (VI). The molecular potentials were observed in preparations under chloralose anesthesia but were depressed in preparations under pentobarbitone anesthesia presumably due to a blockade of the action potentials in the granule cells (Körlin and Larson, 1970; Gordon et al., 1973)

GENERAL DISCUSSION

A. INFORMATION FORWARDED

The CCT and DSCT are largely equivalent tracts which carry information from the fore- and hindquarters, respectively (Oscarsson, 1973). The organization of these paths suggests that they carry information from the periphery about the positions and movements of the limbs. This suggestion has received support from a study of the group I activated component of the DSCT (Arshavsky et al., 1972a). During stepping movements the DSCT neurons have a rhythmic activity which is generated by the input from peripheral receptors activated by the movements in the ipsilateral hindlimb. Also the activity in the ventral spinocerebellar tract and in the spino-reticulocerebellar path relayed in the lateral reticular nucleus is periodically modulated during stepping and scratching movements (Arshavsky et al., 1972a, 1978a, 1978b). However, for the latter paths it was shown that the modulation is generated by central mechanisms and not by a rhythmic activity in the peripheral input. This supports the suggestion that these paths carry information about activity in lower motor centers rather than about peripheral events (Lundberg, 1971; Clendenin et al., 1974a, 1974b; Fu et al., 1977; Illert et al., 1978).

It has been suggested that the SOCPs are internal feedback paths which carry information about activity in lower motor centers in the spinal cord and brain stem (Oscarsson, 1969b, 1973, 1976). This might be the case with the indirect DF-SOCPs which terminate in the c_2 and d_1 zones. These paths have polysynaptic relays which might constitute motor centers. On the other hand, the direct DF-SOCPs which project to the c_1 , c_3 and d_2 zones might carry information mainly related to peripheral events. This is in agreement with the finding that CF responses in Purkinje cells can often be evoked by light tactile stimulation from restricted peripheral fields (Eccles et al., 1972; Leicht et al., 1973; Rushmer, 1976).

The forelimb components of the direct DF-SOCPs have several properties in common with the E-CCT: both systems are activated by cutaneous and high threshold muscle afferents, have disynaptic relays in the MCN, and terminate in sagittal strips which are or-

ganized according to a detailed somatotopical pattern. This supports the suggestion that the direct DF-SOCPs carry information about peripheral events like the E-CCT (II). It is interesting that also the SOCPs which ascend through the ventral funiculus (VF-SOCPs) and terminate in the hindlimb parts of the c_1 and c_5 zones have been suggested to carry peripheral information (Oscarsson and Sjölund, 1977c; Andersson and Sjölund, 1978; Sjölund, 1978). These paths are monosynaptically activated by primary afferents, and the transmission is little influenced by descending control systems. The components of the DF- and VF-SOCPs which project to overlapping areas presumably carry different but complementary information.

An important feature of the IO is the convergence of several afferent paths to the same olivary region. Thus, the olivary neurons projecting to each cerebellar zone in the anterior lobe are activated from two or three SOCPs, from the contralateral sensorimotor cortex, and at least in one case from the contralateral red nucleus (Oscarsson, 1973; Allen et al., 1974; Jeneskog and Johansson, 1977; Ekerot et al., 1979). The convergence occurs at the olivary or possibly in some cases at a preolivary level. It is possible that the olivary relays function as comparators of motor command signals from higher centers and the effects these signals evoke in lower motor centers and the resulting movement (Miller and Oscarsson, 1970; Jeneskog and Johansson, 1977; Ekerot et al., 1979).

B. TERMINATION PATTERNS

It was demonstrated that the DF-SOCP system projects to all the eight sagittal zones in the anterior lobe which have been identified in anatomical and physiological studies (IV). On the other hand the E-CCT projects only to five of these zones (VI). In each zone the parts activated from forelimb nerves through the two paths closely overlap and extend successively more rostrally the more laterally the zone is located (VI, Fig. 5). Thus, the hindlimb and forelimb areas in the anterior lobe are separated by an oblique line rather than by a transverse one as assumed before (Adrian, 1943; Snider and Stowell, 1944; Eccles et al., 1972; Allen et al., 1974).

Each zone has an independent topographical organization. Some of the zones apparently lack somatotopical organization (a , x and c_2) or are only crudely divided into forelimb and hindlimb areas (b and d_1 , cf. Oscarsson and Sjölund, 1977a), whereas some zones (c_1 , c_3 and d_2) have a detailed somatotopical organization. The CF projections are continuous throughout superficial and deep parts of the zones (IV). On the other hand, the MF projections to the superficial and deep cortices are different, being formed by the E-CCT and P-CCT, respectively (III). Different combinations of the CF and MF inputs occur in the different zones. In the superficial cortex of the forelimb part of the c_3 zone there is a close parallelism between the CF and MF inputs which are organized according to a detailed somatotopical pattern. On the other hand, in the deep parts of this zone the same CF input is combined with an MF input through the P-CCT. In the c_2 zone a CF input from several limbs is combined in the superficial cortex with an MF input from the ipsilateral forepaw through the E-CCT, and in the deep cortex with an input through the P-CCT.

The activity evoked through the CCT in the molecular layer was more widespread than in the granular layer due to the spread along the parallel fibers (VI). Our results indicate an effective length of the parallel fibers of about two mm which is in agreement with calculations made by Palkovits et al., (1971). However, a recent anatomical study has shown that the parallel fibers may be considerably longer, 5-7 mm (Brand et al., 1976). Further studies are needed to clarify these discrepancies. The possibility should be considered that the parallel fibers lack or have only few effective synaptic contacts in their peripheral parts.

C. FUNCTIONAL CONSIDERATIONS

It has been suggested that each sagittal zone constitutes a functional unit which controls a certain motor mechanism (Oscarsson, 1973, 1976). The pars intermedia of the anterior lobe which has been the main object of the present studies is known to be important for the control of fine movements in the ipsilateral limbs (Chambers and Sprague, 1955). The detailed somatotopical patterns of the c_1 , c_3 and d_2 zones make it likely that these zones are involved in the control of such motor functions. This control would

be exerted through the anterior interpositus nucleus which receives projections from the Purkinje cells in the c_1 and c_3 zones (Voogd, 1969; Haines and Rubertone, 1977) (the termination of the Purkinje cells of the d_2 zone is unknown). The anterior interpositus nucleus in turn projects to several brain stem nuclei including the red nucleus (McCrea et al., 1978). The abovementioned hypothesis receives additional support from the finding that microstimulation within the anterior interpositus nucleus and within the red nucleus produces contractions in single muscles or groups of related muscles, an effect presumably mediated through the rubrospinal tract (Ghez, 1975). The functional significance of the c_2 and d_1 zones which interdigitate with the c_1 , c_3 and d_2 zones is uncertain.

SUMMARY

1. In the cat a comparison was made of the functional organization and termination of one climbing fiber system, the dorsal spino-olivocerebellar paths (DF-SOCs), and one mossy fiber tract, the cuneocerebellar tract (CCT), which are both activated from primary afferents ascending in the dorsal funiculus. Activity in the paths was evoked by nerve stimulation, and the termination assessed by recording field potentials from the cerebellar cortex. Single unit recordings were also obtained from CCT neurons.

2. The DF-SOCs projected to eight sagittal zones on each side of the anterior lobe. Four zones were activated by cutaneous and high threshold muscle afferents through paths which had disynaptic relays in the dorsal funiculus nuclei (DFN) and direct connections from these nuclei to the inferior olive (IO). Two zones were activated by distal cutaneous afferents through indirect paths which had neurons intercalated between the DFN and the IO.

3. The DF-SOC projection to each zone had an independent topographical organization. Some zones had no, or only a crude somatotopical organization, whereas some zones had a detailed somatotopical organization.

4. The proprioceptive component of the CCT (P-CCT) was monosynaptically activated by group I muscle afferents and originated from the external cuneate nucleus, whereas the exteroceptive component (E-CCT) was di- and polysynaptically activated by cutaneous and high threshold muscle afferents and originated from the rostral part of the main cuneate nucleus.

5. The E-CCT terminated mainly in the superficial parts of the cerebellar cortex at the apices of the folia, whereas the P-CCT terminated mainly in the deep cortex. In the anterior lobe the E-CCT terminated in five sagittal zones which closely overlapped five of the zones activated through the DF-SOCs. In some zones the E-CCT projection had a detailed somatotopical organization which overlapped that of the DF-SOC.

6. The information forwarded by the DF-SOCs and the CCT, the topographical organization of termination zones, and possible roles of these systems in motor control were discussed.

ACKNOWLEDGEMENTS

I want to express my deep gratitude to:

my teacher, Olov Oscarsson, for his generous interest, advice and support throughout this work;

my colleagues at the laboratory for many stimulating and valuable discussions, especially Carl-Fredrik Ekerot and Bengt Sjölund for stimulating collaboration;

David Cooke for stimulating collaboration;

Kersti Andersson, Ilva Bostedt, Olle Hammar, Arne Jönsson, Ulla Leijon and Suzanne Rosander-Jönsson for excellent technical assistance.

The investigations were supported by grants from the Medical Faculty, University of Lund, and the Swedish Medical Research Council (Project No 01013).

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